

DEVELOPMENT OF THE FRUIT-BODY OF A NEW PARASITIC RHIZOPOGON*

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PLATES 1-7

The very remarkable plant described here was first found by us on the roots of *Pinus echinata* and *Pinus taeda* in the winter of 1920. A short report of it was made before the meeting of the North Carolina Academy of Science, May 1, 1920 (14). Since that time it has been under rather constant observation, and fruit-bodies have been found from late summer through the winter. The plant is small and inconspicuous, the fruit-body rarely reaching a diameter of 1.5 cm., yet it shows an interesting case of parasitism and a hitherto unknown method in the development of the fruit-body in a Gasteromycete. Fischer (4) has described the formation of the chambers in *Rhizopogon*, but he did not describe the very young stages.

The work has been carried on under the direction of Dr. W. C. Coker and I wish to express my appreciation of his suggestions, criticisms, and revisions. He is joint author of the species here described. Dr. J. B. Bullitt has been of great assistance in the micro-photographic work. The micro-photographs shown in plate 5 and the lower one in plate 6 were made by him with a simplified micro-photographic apparatus that he designed and made. (This apparatus was described by Dr. Bullitt before the 1923 meeting of the North Carolina Academy of Science.) Dr. Bullitt has also given valuable advice on other micro-photographs, and he cut and stained the material shown in the upper figure of plate 5. Miss Alma Holland has inked in the camera-lucida drawings.

Rhizopogon parasiticus Coker and Totten n. sp.

Fruit-body up to 1.5 cm. broad and high, though usually much smaller, the great majority about 2-5 mm., sometimes almost evenly globose but more often lobed and convoluted; attached at any point to one or several branching, flocculent, rhizomorphous threads which

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run in the humus and connect the fruit-bodies on different roots; rarely some of these branching threads may run along and cohere with the surface of the fruit-body; color of both mycelium and the fruit-body varying from a light ochraceous salmon to a warm buff at all ages until decay sets in. Peridium of mature plants duplex, 50-130 μ thick, the outer layer a spongy mass of loosely woven threads that collapse when the plant is cut or bruised or when decay sets in; the inner layer more closely woven, lighter in color and intimately connected with the internal hyphae; threads of the peridium soft and delicate, 2.6-10.4 μ thick, in young plants more closely woven.

Gleba when fully formed containing many cavities that are minute, irregular, 20-200 μ broad, hollow and lined with the hymenium. Septa 40-115 μ thick, delicate and intimately connected with the peridium, the threads that compose them much branched, segmented, thin-walled, without clamp connections, 2.6-10.4 μ thick and having much the appearance of those of the peridium. The hymenium contains no obvious specialized cystidia, but certain cells among the basidia are of more fusiform shape and these have not been seen to bear spores. One such is shown at the top of figure 7 on plate 7.

Spores brown, fusiform, smooth, 3-3.5 x 7.8-10.4 μ . Basidia short-clavate, 5 x 17 μ , 2-4-spored, with slender sterigmata, which are 2.5-3.5 μ long.

Gregarious and often crowded in large numbers in connected colonies in humus just under or at the surface, and parasitic on rootlets of pine in damp places.

3990. On roots of *Pinus echinata* and *Pinus taeda*, by branch south of Pritchard's, January 10, 1920.

5383. Same place as No. 3990, July 22, 1922.

6051. Roots of *Pinus taeda*, edge of swampy place north of cemetery, January 19, 1923.

6057. Same place as No. 3990, January 28, 1923.

The fruit-bodies arise from a thin, flocculent web of mycelium that surrounds the succulent roots and follows and covers the lateral rootlets, causing them to form a dense glomerulus of very short branches around and in which the fruit-body is formed. The fungal coats of several rootlets soon coalesce into a light buffy mass of various forms and sizes, the ends of the rootlets covered over with the fungal threads give a convoluted appearance to the surface of the young

fruit-body. After full size is reached the mass of rootlets which has occupied by far the greater part of the body is quickly attacked and destroyed by the internal fungus threads and their place is taken by the gleba. In this invasion of the pine tissue the fungus sends first single threads that force their way between the pine cells, as shown in lower figure of plate 4; and then later by repeated branching of these cells the fungus invades in almost solid sheets, as shown in the upper figures of plate 5 and in figure 1 of plate 7. First the cortex region and then the xylem region is completely destroyed. After maturity first the hymenium and then the entire gleba undergoes deliquescence and becomes a dark brown, tasteless slime with a faint odor of iodoform; a very small sub-lobal portion remains sound for a time, but later it too deliquesces. The very delicate peridium soon water-soaks; the outer layer collapses; the inner layer remains for a time as a thin, delicate membrane, the plant then having the consistency of a minute bladder filled with a thin, dark jelly. Later this thin coat disorganizes to allow the escape of the slime.

The true position of this plant is somewhat doubtful. The partly subterranean habit, absence of a capillitium, gleba not becoming a powdery mass, and the indehiscent peridium, would place it in the *Hymenogastrineae*. The absence of a sterile columella excludes it from the *Secotiaceae*. Fischer's (4) drawings of the young fruit-body of *Hysterangium* superficially resemble sections of our young plants, but only superficially for the branching central portion of *Hysterangium* is made up of fleshy strands of fungal material; while this appearance in our young plants is due to the roots of the pine. These roots later disappear entirely. In the *Hysterangiaceae* the whole interior of the fruit-body develops from these fleshy strands and the tramal plates radiate towards the peridium. In our plant growth is from without in, and the tramal plates do not radiate towards the peridium. These are characters of the *Hymenogastraceae*. In this family the presence of the root-like strands below the fruit-body and the absence of the papilla at the end of the spore exclude our plant from *Hymenogaster*; while the smooth, fusiform spores exclude it from *Octaviania*, *Hydnangium*, *Sclerogaster*, and *Lycogalopsis*. The absence of the gelatinous mass in the lobar chambers excludes it from the genus *Leucogaster*; and the hollow chambers with the well defined hymenium exclude it from *Melanogaster*. The soft, loosely woven

character of the peridium that in fresh plants before the collapse of the threads in very old fruit-bodies is far from coriaceous; and the rarity in which the rhizomorphous threads, or fibrils, run along and cohere with the surface of the peridium, throw grave suspicion on the position of this plant in the genus *Rhizopogon*. In this genus, however, the abundance and prominence of these fibrils varies greatly. Zeller and Dodge (17) in their excellent monograph on *Rhizopogon* include in that genus *Rhizopogon maculatus* Zeller & Dodge, a plant with the outer peridium loosely woven. As the method of developing the fruit-body in our plant is so different from anything we have found described, it is quite likely that the plant belongs to an undescribed genus. Yet since so little is known of the development of the other members of this group we have thought it best to describe the plant as a species of *Rhizopogon*.

MYCORRHIZAL CHARACTER

Quite a mass of literature has developed upon the subject of mycorrhizas since Frank's (5 & 6) excellent pioneer works on this subject. He described mycorrhizas on a number of plants, and described the two types of mycorrhizas: *ectotrophic*, or mycorrhiza where the fungal threads do not live within the host cells; and *endotrophic* where the fungal threads do occupy the living host cells. He claimed there was a symbiotic relation between the fungal threads and the host. Even before Frank's papers Tulasne, as pointed out by MacDougal (9), noted that *Elaphomyces* forms coatings on the roots of pine. MacDougal takes this reference from Tulasne's *Fungi Hypogaei*, 1851. We have not examined this edition; but in the edition of 1862 (15) Tulasne does not name the pine as the host of *Elaphomyces*; but he does have quite a discussion as to whether the *Elaphomyces* is parasitic on the tree rootlets or whether, as Vittadini had suggested, the rootlets profited by the presence of the fungus. He concludes that the parasitism of *Elaphomyces* is very problematical, if not improbable for the greater number of them. Groom (7) showed that there is a mutual exchange of material between the host and fungus in the mycorrhiza of *Thismia*, and claimed that the weight of evidence at that time supported the symbiotic view of mycorrhizas as held by Frank, but he says: "Mycorrhiza is, then, either a highly adapted and symbiotic community beneficial to both symbionts, or it is a pure matter of infection of a plant by a fungus, and there is a constant struggle

between the host and the would be parasite." In support of this last view he calls attention to the fact that E. Bruns (2) had shown that *Polysaccum* causes an ectotrophic mycorrhiza of pine roots, and that "some of the hyphae actually dip deep into the tissue of the root, at the same time absorbing so vigorously as to play havoc with the infected tissues."

The earliest observers of mycorrhizas thought that *Elaphomyces* and tubers or truffles caused all the ectotrophic mycorrhiza. Gradually the list of fungi known to cause mycorrhiza has been enlarged. MacDougal (9) in 1899 gave a list of the fungi known at that time to produce mycorrhiza. The list included species of *Fusiporium*, *Eurotium*, *Pythium*, *Nectria*, *Celtidia*, *Elaphomyces*, *Polysaccum*, *Geaster*, *Boletus*, *Lactarius*, *Cortinarius*, *Tricholoma*, and *Agaricus*. Of these *Elaphomyces*, *Polysaccum*, *Geaster*, *Boletus*, *Tricholoma*, and *Agaricus* formed mycorrhizas with the conifers, some of these with other plants too. Kauffman (8) has shown that *Cortinarius rubipes* forms mycorrhizas on red oak, sugar maple, and *Celastrus scandens*. Pennington (13) in 1910 reported that a species of *Cortinarius* and "probably a form of *Russula emetica*" produced mycorrhizas upon the red oak, and that *Boletus speciosus* and *Tricholoma transmucans* produced them upon the black oak. McDougall (10) added four species to the known list of ectotrophic mycorrhiza-forming fungi: *Russula* sp. on *Tilia americana*, *Boletus scaber fuscus* on *Betula alba* var. *papyrifera*, *Cortinarius* sp. on *Betula alba* var. *papyrifera*, and *Scleroderma vulgare* on *Quercus alba*. He showed that at least four, and probably more, different species of mushrooms may form mycorrhizas on the same tree. He also showed that the endotrophic mycorrhizas of the maples are sometimes symbiotic associations, and sometimes associations in which the fungus is surely a parasite of the roots; but that the ectotrophic mycorrhizas of forest trees are not symbiotic associations, but instances of parasitism of fungi on the roots of trees. This opinion is reiterated in a later paper (12).

There has probably been more research and publications on the endotrophic mycorrhizas than for the ectotrophic forms. Many of them seem to show real symbiosis, or what McDougall (11) terms "reciprocal parasitism." The *Orchidaceae* and *Ericaceae* show generally a mycorrhizal condition. MacDougal (9) says that Warhlich examined 500 species of Orchids in cultivation at Moscow and found

all exhibiting mycorrhiza. Bower (1) says that the seedlings of the common heather (*Calluna vulgaris*) will not develop roots until infected with the right fungus. Our plant, however, clearly forms the ectotrophic mycorrhiza, and no attempt will be made in this paper to review the extensive literature on the endotrophic mycorrhizas.

In 1922 McDougall (12) reported a *Cortinarius* sp. with yellow mycelium forming mycorrhiza on *Picea rubra* and one with white mycelium on *Abies Balsamea*. He also described a tubercle-like compound mycorrhiza on seedlings of *Pinus strobus* from Maine. He says: "So far as I am aware no structures at all similar to these have ever before been described. Coral clusters of mycorrhizas containing large clusters of rootlets are well known. Moller reported a cluster on a spruce seedling that, judging from his illustrations, must have contained altogether a total of a hundred or more rootlets and I have frequently seen comparable if somewhat smaller clusters on the roots of oak and hickory species. The case that we are reporting here, however, in which the rootlets are bound together by the mycelium into a compact tubercle seems to be entirely unique." The nodules were pale yellow or buff in color and varied from one to four millimeters in diameter. No sporophores were found. His sketch of a cross section of this compound mycorrhiza agrees very well with sketches of our plants. There is also an agreement in color; but we find plants much larger, up to 1.5 cm. in diameter, and we do find sporophores. There is quite a possibility that McDougall had the same plant that we have found on *Pinus echinata* and *Pinus taeda*.

Dr. Collier Cobb (3) in his paper entitled *The Forests of North Carolina* mentions the presence of minute fungi attached to the roots of *Pinus taeda* on Hatteras Island and suggests that the trees may be aided by their presence. I have shown our plants to Dr. Cobb and he is of the opinion that they are the same plants observed by him on Hatteras. He says that he mentioned them in a talk entitled "Hatteras Island" before the 44th meeting of the Elisha Mitchell Scientific Society at Chapel Hill, December 9, 1902; and in one entitled "Hatteras Island and Its Shifting Sands" before the Association of American Geographers in New York in 1906. If McDougall's plants from Maine and those observed by Cobb on Hatteras Island are *Rhizopogon parasiticus*, then this species has quite a wide range. It is so easily overlooked that closer observation may show it to be not uncommon generally.

Rhizopogon parasiticus forms a compound ectotrophic mycorrhiza; but the mycorrhizal character is short lived and the mass of inclosed rootlets is completely absorbed. The fungus then forms its fruiting surface right in the position that the obliterated pine tissues had held. In the literature cited above we have found no reference to a fruit-body formed in this way. Wolf (16) has shown that the Tuckahoe or Indian-bread is formed by *Poria Cocos* attacking the pine root and forming a large sclerotium within the bark of the root. Later, under certain conditions, a poroid, resupinate fruit-body is formed on the surface of the sclerotium. This *Poria*, though not a mycorrhizal fungus, does make an interesting comparison with our plant in that it replaces much, though not all, of the pine tissue of the root.

SUMMARY

1. A new fungus of the *Hymenogastraceae* is described and given the name of *Rhizopogon parasiticus*, though doubt is expressed as to whether the plant is correctly placed in the genus *Rhizopogon* or whether it belongs to an undescribed genus.

2. A review of the work on ectotrophic mycorrhizas is given, and *Rhizopogon parasiticus* is shown to form compound ectotrophic mycorrhizas on the roots of *Pinus echinata* and *Pinus taeda*.

3. *Rhizopogon parasiticus* gives further proof of the parasitic nature of ectotrophic mycorrhizal forming fungi, for the pine tissues of the rootlets invaded by this fungus are completely destroyed.

4. The plant is unique in the way it forms the sporophore, forming a gleba in the space formerly occupied by the invaded cluster of pine rootlets.

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EXPLANATION OF PLATES

(Rhizopogon parasiticus)

PLATE 1

Fruit-bodies of various ages on roots of pine. Natural size.

PLATE 2

Clusters of fruit-bodies showing the rhizomorphic threads. x 6.

PLATE 3

(Above) A longitudinal section through a cluster of infected pine rootlets, showing the cluster completely surrounded with fungal threads, also the cortical area of the rootlets invaded. x 40.

(Below) A cross section through a cluster of infected rootlets of same age as in fig. 1. x 40.

PLATE 4

(Above) A longitudinal section through a small root showing parts of three clusters of rootlets surrounded with fungal threads, of same age as shown in plate 3. x 24.

- (Below) A more highly magnified view of a part of the section shown in lower figure of plate 3. The infecting fungus can be seen invading the cortical area in single threads. x 190.

PLATE 5

- (Above) Section through a plant older than the one in plate 4. The hyphae are now invading in almost solid sheets along the cell walls. x 240.
- (Below) Longitudinal section of a fully grown fruit-body, showing hymenial chambers, the pine tissue completely destroyed. x 55.

PLATE 6

- (Above) Showing tramal plates, hymenium, and chambers. x 250.
- (Below). Part of above. Sterigmata can be seen near the middle of the figure. x 500.

PLATE 7

- Fig. 1. Fungal threads attacking cortical cells of the pine, in same stage as shown in upper figure on plate 5. The fungal threads force their way between and over the pine cells which are the unshaded areas in the figure. x 690.
- Figs. 2 & 3. Basidia with nearly mature spores.
- Fig. 4. Young basidia. x 1290.
- Fig. 5. Mature spores. x 1290.
- Fig. 6. Tramal thread, showing nuclei. x 1290.
- Fig. 7. Trama and hymenium of mature plant, some of the basidia with two, others with four sterigmata. x 1290.
- Figs. 4-6 stained to show nuclei.